Anthopleura sola, a new species, solitary sibling species to the aggregating sea anemone, *A. elegantissima* (Cnidaria: Anthozoa: Actiniaria: Actiniidae)

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Abstract.—The Sunburst Anemone, a common inhabitant of rocky shores in central and southern California, is here designated as *Anthopleura sola*, new species. This large, conspicuous, solitary sea anemone was previously considered a non-clonal variant of the well-known, clonal Aggregating Anemone, *A. elegantissima*. Although polyps of these two species are similar in appearance and in cnidae, documented differences in population genetics, ecology, biogeography, development, and life history are evidence of a recently evolved sibling-species pair. Where the two species co-occur, they are readily distinguished in the field by differences resulting from their different life histories. In *A. elegantissima*, longitudinal fission results in aggregations of small polyps. *Anthopleura sola* does not divide and instead grows into larger, isolated individuals that have more often been confused with specimens of the Giant Green Anemone, *A. xanthogrammica*.

The sea anemone *Anthopleura elegantissima* (Brandt, 1835), abundant in the rocky intertidal of the northeastern Pacific, has long been recognized as including two sorts of individuals (Hand 1955)—some larger and solitary and some smaller and aggregated. A recent analysis of genetic variation in allozymes by McFadden et al. (1997) has confirmed earlier evidence (Francis 1979) that they belong to two distinct species. Here, we formally designate the solitary form as a new species.

In *A. elegantissima*, repeated episodes of longitudinal binary fission result in clonal aggregations of relatively small individuals. In the solitary polyps of the new species, fission does not occur, and larger, isolated individuals result (Hand 1955, Francis 1979). The presence or absence of fission in the life history yields animals that are readily distinguishable in the field by their

size and aggregated vs. solitary distribution (Fig. 1).

Despite some doubt that the name *A. elegantissima* is properly applied to the most common small intertidal anemone of California [see Cutress (1949) and Hand (1955) for discussion of problems with the original description], this name is so well established in the literature that it should be conserved for the clonal species. No grounds support using this name for the solitary species we are establishing.

Materials and Methods

Specimens of *Anthopleura sola* and *A. elegantissima* were collected at Soquel Point and the breakwater at the Santa Cruz Yacht Harbor, Santa Cruz County, California in summer and autumn, for analysis of cnidae. Cnidae were described (by LF) from both fresh and formalin-preserved

specimens selected to cover a broad range of individual sizes.

To measure cnidae, a sample of tissue was macerated mechanically in a drop of seawater and pressed into a thin layer between a slide and coverslip. Such smears were prepared from tentacles, acrorhagi, column, actinopharynx, and mesenterial filaments for 6 specimens of each species and examined using a light microscope with differential interference contrast optics at 1000× and oil immersion. Measurements were to the nearest 0.3 μm using an optical micrometer, and to the nearest 0.1 μm using a computer-linked video camera (image analysis) system.

Measurements were reported separately for cnida types from different parts of the body and also for any subsets that consistently showed strongly discontinuous, variation in shape or size (see 17 categories of data in Table 1). Each slide was scanned systematically (as described by Williams 1996), and the maximum length and width of individual capsules were measured (method of Hand 1954) to establish size ranges. All capsules were measured until the sample size for the most common types or shape variants of the cnidae reached at least 20. For the less common cnidae, an effort was made to measure at least 10. Finally, the slides were rapidly scanned in search of rare cnidae and also any of the more common ones that looked substantially larger or smaller than those already measured. Only clearly visible, intact, unfired capsules with their long axes lying roughly in the plane of the slide were measured.

Family Actiniidae Rafinesque, 1815
Genus *Anthopleura* Duchassaing & Michelotti, 1860
Anthopleura sola, new species
Figs. 1, 2

Morphology and development.—Hand (1955) included *Anthopleura sola* in his thorough description of *A. elegantissima*, characterizing the shape and coloration of the animals (including the mouth, oral disc, tentacles, column with acrorhagi and verrucae, and pedal disc) and the histology and internal anatomy (including the arrangement of mesenteries, the shape and position of muscles and gonads, the nature of epithelial layers and mesoglea, and the size and distribution of cnidae).

Anthopleura sola shares the morphological characters of *A. elegantissima*, except that *A. sola* is non-clonal and its polyps are large, growing to ~20–25 cm across the tentacle crown. As they do not divide and lack fission scars, regularly arranged mesenteries are to be expected. Given the anatomical similarity between *A. elegantissima* and *A. xanthogrammica*, two well-recognized species with differences in external morphology and in cnidae, repeating Hand's histological work in a search for differences at the anatomical level between *A. elegantissima* and *A. sola* seems unwarranted. No differences between *A. sola* and *A. elegantissima* emerged from our study of cnidae (see below).

Polyps of *A. sola* occur as separate male and female individuals, as do clones of *A. elegantissima*. Females of *A. sola* were observed to spawn (in June, in a large outdoor tank, Santa Cruz, California) at the same time as those of *A. elegantissima*, and the gametes of both species were similar in size and appearance (J. S. Pearse, pers. comm.). Annual sexual reproduction has been studied only in *A. elegantissima* (e.g., Ford 1964, Jennison 1979, Sebens 1981), which is not an asexual lineage or in any way less sexual than *A. sola*, but a normal, sexual species whose individuals grow by replication of many small polyps (e.g., Tsuchida & Potts 1994). The polyps of a clonal aggregation, though disconnected, are comparable to the many polyps of a growing coral colony, in that both result from the development of a unique zygote and represent the growth of one genetic individual (see Pearse et al. 1989, Wasson & Newberry 1997). In contrast, individuals of *A. sola*
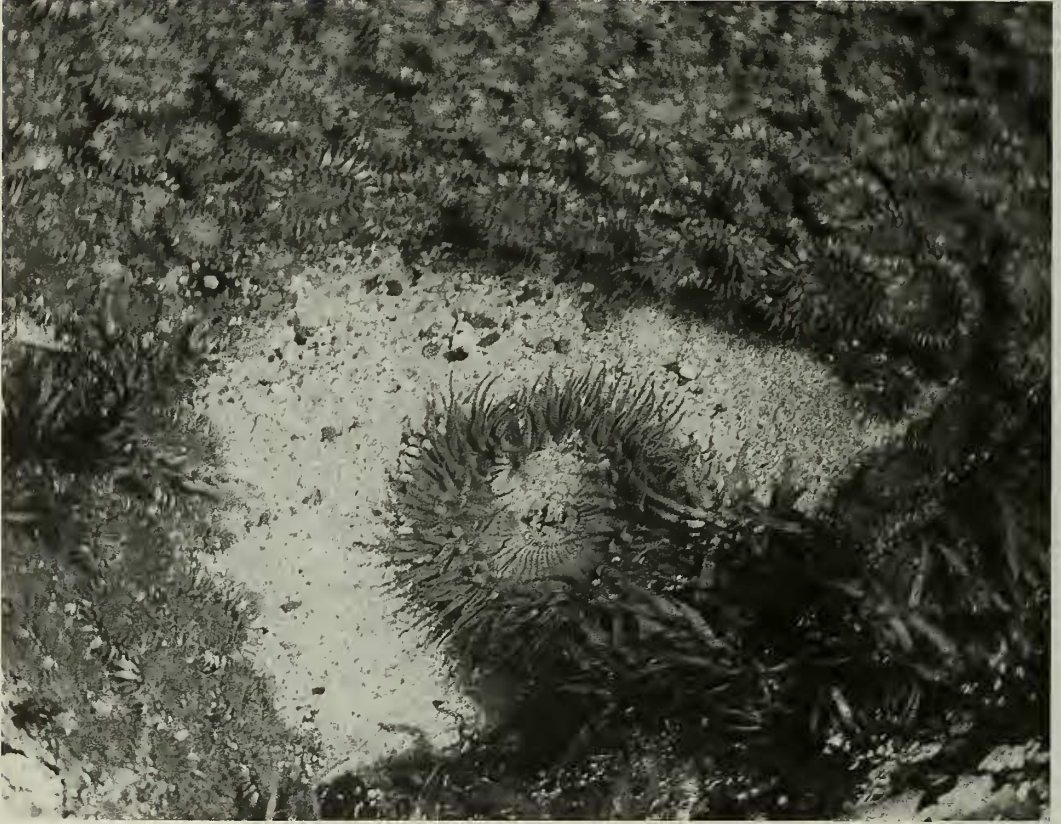
Fig. 1.   A large solitary specimen of *Anthopleura sola*, new species, about 12 cm across the crown of tentacles, surrounded by a clonal aggregation of *A. elegantissima* in the intertidal at Soquel Point, Santa Cruz, California. (Courtesy J. S. Pearse)

grow into a single large polyp—a major morphological and developmental difference from *A. elegantissima*. The separate identities of the two species are further reinforced by ecological differences and confirmed by evidence for genetic differences (see Discussion).

Cnidom.—Spirocysts, holotrichs, basitrichs, and microbasic p-mastigophores.

Size and distribution of cnidae.—The shapes of the cnidae and their locations within the polyp were the same for *Anthopleura sola* and for *A. elegantissima*. Besides those listed and illustrated by Hand (1955:57–59), we distinguished a third category of relatively rare acrorhagial holotrichs (Fig. 2a, b; a, b in Table 1), especially in the tips of smaller, poorly developed acrorhagi. These were similar to the common,

more slender ones described by Hand (1955, fig. 13D) but most were shorter and more strongly tapered; the tubule, close to its apical point of attachment with the capsule, was more tightly coiled. Like Hand (1955), we identified basitrichs of two shapes in the pharynx, one a slender cylinder of uniform width (Fig. 2c, d), the other typically not of uniform width, often with a bulbous swelling either in the middle or at the base (Fig. 2e, f). In our material, however, the slender cylindrical one was shorter, the bulbous one longer (Table 1)—proportions differing from those recorded by Hand (compare fig. 13J and 13I, respectively). Individual bulbous capsules varied considerably in shape.

For each of our 17 categories of data, size ranges were overlapping but different

in the two species (Table 1). Both maximum length and minimum length were greater in *A. sola* than in *A. elegantissima* for 13 of the 17. Polyps of *A. sola* are typically larger than those of *A. elegantissima*: wet weights for specimens of *A. sola* examined were 56.3 ± 74.8 (mean ± SD, range 2.03–205 g) and for *A. elegantissima* 2.17 ± 2.61 (mean ± SD, range 0.04–5.93 g). The subtle differences in the size ranges of cnidae reported here seem to relate mostly to polyp size and, consequently, are probably not useful as diagnostic characters for separating these two species.

Type material and locality.—*Anthopleura sola*, new species. Holotype: One solitary polyp, found isolated from any others. Pedal disc, 4 × 7 cm. Collected 30 Dec 1998 in the mid-intertidal zone at Soquel Point, Santa Cruz, California (36°57.15′N, 121°58.29′W) by Vicki Pearse. Holotype (CASIZ 116500) preserved in seawater formalin and deposited in the collections of the California Academy of Sciences, Dept. of Invertebrate Zoology, Golden Gate Park, San Francisco, California 94118, USA. Paratypes, all collected on the same date at the type locality. Deposited at the CAS: two paratypes preserved in seawater formalin (CASIZ 116501 and 116502) and two paratypes preserved in ethanol (CASIZ 116503 and 116504). Deposited at the Santa Barbara Museum of Natural History, Dept. of Invertebrate Zoology, Santa Barbara, California 93105, USA: one paratype preserved in seawater formalin (SBMNH 345318) and one paratype preserved in ethanol (SBMNH
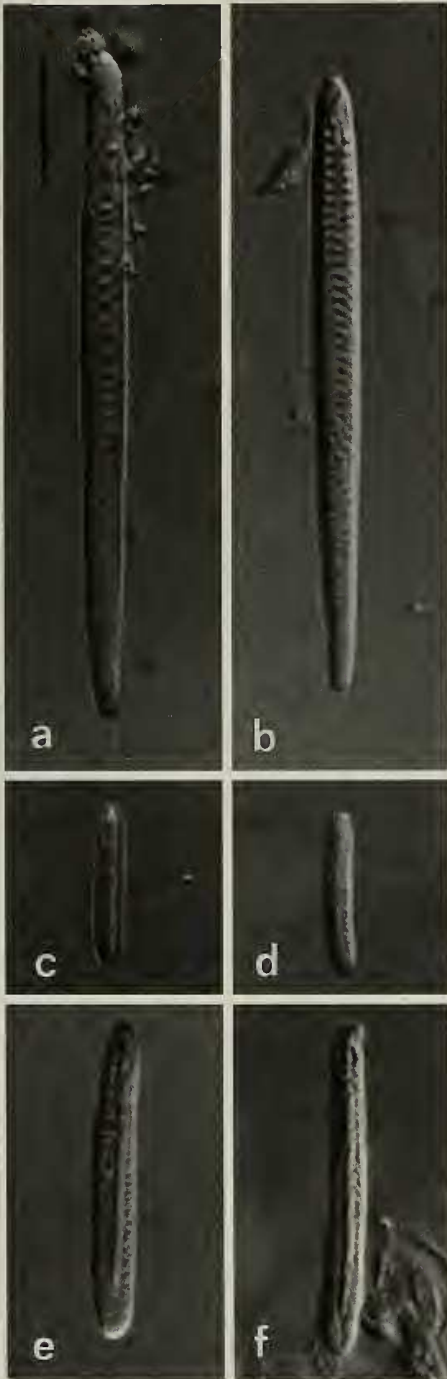
Fig. 2. Some nematocysts found both in *Anthopleura sola*, new species (left: a, c, e) and in *A. elegantissima* (right: b, d, f), photographed at 1000× magnification. All at the same scale (scale bar, 10 μm) and shown with the apex (tubule-bearing end of the capsule) uppermost. (a, b) An acrorhagial holotrich

←

different from both of the more common ones illustrated by Hand (1955, fig. 13D, E). (c, d) The shorter of our two categories of pharyngeal basitrichs, the capsule a slender cylinder of uniform width, although sometimes curved, as in 2d. (e, f) The longer and more common of our two categories of pharyngeal basitrichs, the capsule typically not of uniform width, many with a bulbous swelling (e.g., bottom of 2f). In smears, the cnidocyte often formed another conspicuous bulge at the capsule apex (top of 2f).

Table 1.—Cnidae of *Anthopleura sola* and *A. elegantissima*. Ranges of lengths and widths of cnidae (17 categories of data by location within the polyp, shape, and size) in the tentacles, acrorhagi, column, actinopharynx, and mesenterial filaments. Samples: the ratio indicates the number of polyps in which each cnida was found out of the 6 polyps of each species examined; the second value indicates the number of capsules measured in all polyps. The uppercase letters A–P designate the corresponding 16 cnidae illustrated for *A. elegantissima* by Hand (1955), fig. 13. The lowercase letters a–f refer to our Fig. 2. The additional category of acrorhagial holotrichs was less common and not measured separately by Hand. The cnidae that were termed atrichs (Hand 1955) do bear minute spines along the thread and are considered to be holotrichs.

| Categories | *Anthopleura sola* | | *Anthopleura elegantissima* | | |
	Length × width (μm)	Sample	Length × width (μm)	Sample	Figure ref.
Tentacles:					
Spirocysts	13.0–35.0 × 2.0–4.0	6/6: 135	12.0–31.0 × 2.0–4.5	6/6: 120	A
Basitrichs	12.5–33.0 × 1.3–4.0	6/6: 135	14.0–28.5 × 2.0–3.0	6/6: 110	B
Acrorhagi:					
Spirocysts	22.0–45.0 × 2.0–4.0	6/6: 115	14.7–36.4 × 1.8–3.8	6/6: 85	C
Holotrichs	41.0–102.0 × 2.0–5.5	6/6: 135	38.0–89.0 × 2.5–5.0	6/6: 120	D
Holotrichs	59.0–104.0 × 4.8–10.0	6/6: 133	45.5–90.0 × 4.5–10	6/6: 102	E
Holotrichs	34.0–78.0 × 2.8–5.0	4/6: 15	27.7–64.0 × 2.3–4.8	5/6: 49	a,b
Basitrichs	10.0–20.5 × 1.5–3.0	5/6: 52	5.8–28.0 × 1.0–3.0	5/6: 50	F
Column:					
Holotrichs	19.0–28.0 × 3.0–4.0	2/6: 11	15.0–20.5 × 3.0–5.0	4/6: 15	G
Basitrichs	9.5–24.0 × 1.5–3.0	6/6: 135	7.5–16.5 × 1.5–3.3	6/6: 120	H
Actinopharynx:					
Basitrichs	6.0–27.0 × 1.0–3.0	6/6: 113	10.0–19.0 × 1.3–3.0	6/6: 109	I,J?, c,d
Basitrichs	19.0–31.0 × 1.8–5.0	6/6: 130	18.0–31.0 × 2.0–4.5	6/6: 118	I,J?, e,f
Microbasic p-mastigophores	20.0–30.0 × 3.5–6.5	6/6: 108	17.0–28.0 × 4.0–6.0	6/6: 108	K
Filaments:					
Basitrichs	8.5–23.0 × 1.0–3.0	5/6: 114	7.0–13.5 × 1.5–3.0	6/6: 90	L
Basitrichs	28.5–50.0 × 4.5–8.5	6/6: 131	22.0–42.0 × 4.5–9.0	6/6: 104	M
Basitrichs	20.0–33.0 × 1.0–1.5	3/6: 7	29.0–39.0 × 1.0–1.5	4/6: 27	N
Microbasic p-mastigophores	12.0–19.0 × 1.8–4.0	3/6: 7	13.0–30.0 × 2.0–4.5	6/6: 89	O
Microbasic p-mastigophores	20.5–34.0 × 3.8–7.0	6/6: 135	17.0–29.0 × 4.0–5.5	6/6: 120	P

345319). Deposited at the University of Kansas Natural History Museum, Lawrence, Kansas 66045, USA: one paratype preserved in seawater formalin (UKNHM 01208) and one paratype preserved in ethanol (UKNHM 01209).

For comparison, several voucher specimens of *Anthopleura elegantissima*, all collected on the same date and at the same site as the holotype and paratypes of the new species (see above), were also deposited in the collections of the CAS: One polyp from within a cohesive aggregation of many polyps, taken to be a clone because of the intimate contact and identical coloring of its members. Pedal disc, 3 cm. Preserved in seawater formalin (CASIZ 116505). Additional specimens from the same clone: three polyps preserved in seawater formalin (CASIZ 116506) and three polyps preserved in ethanol (CASIZ 116507); pedal discs, 2–3 cm.

Etymology.—From the Latin *sola* ("alone"), referring to the solitary, nonclonal condition, which distinguishes individuals of this species from polyps of the aggregated, clonal *A. elegantissima*. The species name *sola* relates also to the often strikingly pigmented mesenterial insertions and other radial, sun-like (Latin *sol*, "sun") oral disc patterns, which distinguish the disc in this species from the typically unmarked, uniformly blue-green oral disc in *A. xanthogrammica*, which is also large and non-clonal. For *Anthopleura sola*, we recommend the common name "Sunburst Anemone."

Previous references.—The other three northeastern Pacific species of *Anthopleura* (*A. artemisia, A. xanthogrammica, A. elegantissima*) are not being synonymized with the new species, but their names have often been misapplied to it. In the examples listed below, the specific pages and figures cited discuss or illustrate specimens of the new species presented under these older names.

Anthopleura artemisia (Dana, 1846:149–150).—Stephenson & Stephenson, 1972: 235. In a study of the Monterey Peninsula, carried out in 1947.—Hinton, 1987: 55–57, pl. 26.

Anthopleura xanthogrammica (Brandt, 1835:212)—Johnson & Snook, 1935: fig. 79, pl. IV. as *Cribrina xanthogrammica.*—MacGinitie & MacGinitie, 1949, 1968: fig. 16.—Hedgpeth & Hinton, 1961:42, fig. 24.—Hedgpeth, 1962:54 (figure).—Braun & Brown, 1966:22, 24–25.—Ricketts & Calvin, 1968: fig. 53.—Hinton, 1969:53–54, fig. 27, pl. 4. 1987: 55–57, fig. 27, pl. 24.—Snyderman, 1987:77, pl. A-3, no. 9.—Davis, 1991:63, pl. 68.

Anthopleura elegantissima (Brandt, 1835: 213). Only the larger, solitary individuals referred to in the following references belong to the new species.—Hand, 1955: 54–61; see discussion of synonymy, pp. 60–61. 1975:88, 90, 91.—Francis, 1973a, 1973b, 1979, 1988.—Pearse, 1981:216. This photo and the one of *A. xanthogrammica* on the same page illustrate the differences between these species.—Walsh, 1981a.—Annett & Pierotti 1984:204.—Ricketts et al., 1985: fig. 69 (same as fig. 53 in 1968 edition, relabeled.).—Smith & Potts, 1987.—Harris, 1991.—Gotshall, 1994: fig. 51. This photo and the one of *A. xanthogrammica* on the same page illustrate the differences between these species.—Barry et al., 1995:672, 673.—Snyderman, 1998:10 (figure).—Walton, 1998.—Sagarin et al., 1999.

Anthopleura sp. In both references listed here, this designation refers to the new species. McFadden et al., 1997. This study of >800 clonal and non-clonal specimens concluded that the two represent reproductively isolated taxa and referred to the latter as *Anthopleura* sp. throughout.—Secord & Augustine, 2000 also referred to *Anthopleura* sp.

Anthopleura sola.—Shick et al., 1996. The name was used as a nomen nudum in anticipation of its formal designation in the present paper and refers to large solitary

specimens of the new species collected by J. S. Pearse at the type locality.

Discussion

Distribution and interactions with other species.—*Anthopleura sola* tends to thrive in relatively sheltered positions and moderate climes. On a microhabitat scale, these sea anemones usually occupy protected places in quiet pools, at the bases of boulders, and in rock pockets and crevices, seldom on flat rock surfaces (Francis 1979, Harris 1991). Even when much of the pedal disc occupies a flat surface and can be relatively easily detached, a slender toe-like projection from the disc commonly retains a strong anchor-hold in a small hole in the rock (this study and L. G. Harris, pers. comm.), probably the cavity in which the young animal originally settled, long since outgrown. In the subtidal, and sometimes in the intertidal, the anemones are found attached to rocks in sand, the oral disc flush with the sand surface (Harris 1991). This species occurs typically in bays, but also on the open coast, in the middle to low intertidal and into the subtidal (Francis 1979), being found commonly to at least 10 m (Harris 1991, J. S. Pearse, pers. comm.). Its range is along the Pacific coast of North America at least from northern Mexico at Punta Banda, Baja California, to just north of San Francisco Bay at Doran Rocks near Bodega Bay, California (Francis 1979, McFadden et al. 1997).

Harris (1991) discussed possible effects on the species' distribution by predators, which include the sea star *Dermasterias imbricata* and the nudibranch *Aeolidia papillosa*. The large polyps of *A. sola* appear to have an advantage over the smaller ones of *Anthopleura elegantissima*, which are more successfully approached and attacked by these predatory species. Large size is probably the critical factor that permits *A. sola* to occupy subtidal depths that are beyond the vertical range of *A. elegantissima*. Annett & Pierotti (1984) described numerous occasions on which an "exceptionally large" individual (=*A. sola*) repelled attacks by *D. imbricata*, whereas small individuals of *A. elegantissima* were more readily devoured. Small individuals of the nudibranch *Aeolidia papillosa* thrived when feeding on *A. elegantissima* but could not be raised on *A. sola*; they stopped eating and died (L. G. Harris, pers. comm.). In the subtidal, individuals of *A. sola* surrounded by sand may be partially protected from sea-star predation, but can suffer predation by larger individuals of *A. papillosa* (see Harris 1991).

Zooxanthellae occur as endosymbionts in *A. sola*, as they do also in *A. elegantissima* and *A. xanthogrammica* throughout their ranges. We know of no instance of zoochlorellae occurring in *A. sola*, and, on the basis of the virtually non-overlapping distribution of this anemone species with that of the green symbionts, we do not expect zoochlorellae to be found in this species. The southern limit so far observed for symbiotic zoochlorellae in *A. xanthogrammica*, the area of Bodega Bay and nearby Dillon Beach, corresponds to the northern limit of *A. sola*, and the southern limit observed for zoochlorellae in *A. elegantissima* is central Oregon (Secord 1995, Secord & Augustine 2000). South of these limits, zooxanthellae are the only photosynthetic microalgae symbiotic in *A. xanthogrammica* and *A. elegantissima*. The striking coincidence of the northern limit of *A. sola* and the southern limit of zoochlorellae may hold significant clues to the biology of both the sea anemones and the symbionts.

Similar species.—Three other species of *Anthopleura* are recognized within the range of *A. sola*. Individuals of all four species may be found living within a meter of each other on rocky intertidal shelves along the central California coast, and the observations below relate to specimens from this region.

Anthopleura artemisia, the Moonglow Anemone. Stephenson & Stephenson (1972) presented an elegant and unambig-

uous account of the appearance of *A. sola*, recognizing it as an entity separate from *A. xanthogrammica* and *A. elegantissima*, but under the name *A. artemisia*. Despite occasional references to *A. sola* as *A. artemisia* (see examples in Previous references, above), the latter species was clearly described by Hand (1955) and is readily distinguished from the other local species. Of the four California species of *Anthopleura*, this is the only one in which photosynthetic endosymbionts are not regularly, if ever, present (Hand 1955); the two published reports of zooxanthellae (Haderlie et al. 1980, Walsh 1981b) have a dubious basis (C. Hand, pers. comm.; P. J. Walsh, in litt.). Unlike the other three species, which are primarily green, individuals of *A. artemisia* with any green coloring are uncommon in central California. In all four species, the green color is an animal pigment, not produced by symbiotic algae (Buchsbaum 1968). *Anthopleura elegantissima* and *A. xanthogrammica* may have zoochlorellae that also contribute green coloring, but only in the northern part of their ranges, as discussed above. The body color of *A. artemisia* is typically dull gray or brown; the oral disc and tentacles are variously colored (neutral tones and shades of red are common) and the color is either solid or patterned with white. These anemones are seen most often as isolated individuals attached within deep holes in rock, or attached to rocks beneath the sand so that only the oral disc is visible. However, longitudinal fission has been observed, resulting in small clones, and the aftermath of fission is evident in irregularities of the acrorhagi, tentacles, and mesenteries (Hand 1955 and pers. comm., Haderlie et al. 1980); cloning has yet to be confirmed by genetic data from field populations. In addition to traits mentioned above, several differences in complement and distribution of cnidae distinguish *A. artemisia* from all three other local species of *Anthopleura*. The diversity of holotrich shapes is less in *A. artemisia*, while that of basitrichs is greater and the

distribution within the polyp also differs (see Table 1 and Hand 1955, figs. 11, 13, 15). For example, *A. sola*, *A. elegantissima*, and *A. xanthogrammica* share the absence of one basitrich category present in *A. artemisia* and at least two other actiniids, *Epiactis prolifera* and *Urticina* (=*Tealia*) *coriacea* (see Hand 1955, figs. 9, 19). *Anthopleura artemisia* was reported by Hand (1955) as occurring from Japan(?) and Alaska to southern California.

Anthopleura xanthogrammica, the Giant Green Anemone. This species is the one most commonly confused with *A. sola*, as both are large, greenish, solitary anemones. However, expanded polyps of *A. xanthogrammica* are easily distinguished by their uniformly green or blue-green oral disc and tentacles, lacking the white tentacle bars and other colored stripes and markings on the tentacles, as well as the strikingly pigmented mesenterial insertions and other radial oral-disc patterns, typical of *A. sola* (and *A. elegantissima*). By inserting a finger, one can feel the firm, strong mouth of *A. xanthogrammica*, whereas the mouth is a soft loose opening in *A. sola*. Likewise, the softness of the body of *A. sola* (and *A. elegantissima*) contrasts with the much firmer, less compressible body of *A. xanthogrammica*. Moreover, the column of *A. xanthogrammica* is densely covered with compound verrucae, not arranged in rows, in contrast to the vertical rows of verrucae that are simple on most of the column, compound only on the collar in *A. sola* (and *A. elegantissima*). Below the limbus, the smooth, thin pedal disc of *A. xanthogrammica* typically spreads well beyond the column diameter and is roughly circular in outline, in contrast to the pedal disc of *A. sola*, which is thicker, less regular in outline, and little larger than the column diameter. Despite all these differences, *A. sola* has so often been identified as *A. xanthogrammica* that caution is indicated in interpreting older literature. For example, Barry et al. (1995) and Sagarin et al. (1999) reported a dramatic increase in *A. sola* and decline in

A. xanthogrammica, at a site on Monterey Bay, California, based on comparing their data with those from a 60-year-old study that very likely confused individuals of these two species. In this case, their conclusion is probably correct, based on our experience at the same site over 30 years, but the quantitative comparison is undermined by the taxonomic uncertainties. *Anthopleura xanthogrammica* occurs from Japan(?) to southern California (Hand 1955), but south of Point Conception, it is restricted to a few areas of cooler water near the heads of submarine canyons (Francis 1979).

Anthopleura elegantissima, the Aggregating Anemone. Polyps of this clonal species, when kept submerged and heavily fed in the laboratory, sometimes grow rapidly without dividing and reach sizes not seen in the field. However, such polyps differ in appearance from specimens of *A. sola* of comparable size. The lab-grown clonal polyps look like greatly inflated versions of smaller ones. The tentacles, oral disc, and body wall are translucent. Both the tentacles and the verrucae of the column are large in proportion to the body, and their number does not appear to increase, so that relatively large spaces occur between the rows. Compared to the verrucae of non-dividing specimens of *A. elegantissima*, those of *A. sola* are smaller in proportion to body size and occur in many more, densely packed rows.

In the field, *Anthopleura sola* is usually easy to distinguish from *A. elegantissima*. The most useful clues for separating these species are related to their development and distribution. *A. sola* has non-clonal development: it does not divide and so lacks fission scars; therefore, barring injury, its polyps should have regularly arranged mesenteries. Its polyps grow to large sizes, and they live singly and out of physical contact with neighboring anemones. In contrast, *A. elegantissima* replicates by longitudinal fission, which produces temporary scarring on the columns of recently divided individuals and long-lasting irregularities in the arrangement of mesenteries (Hand 1955). Fission typically results in smaller anemones, living in more or less compact aggregations of clonemates in contact with each other.

Besides the primary difference in life history—non-clonal vs. clonal development—the two species differ in habitat and biogeographic range. Whereas *Anthopleura sola* is typically found in lower and more protected situations, as described earlier, *A. elegantissima* predominates on open rock surfaces in high to mid-intertidal zones (Francis 1979) and rarely extends to subtidal depths (L. G. Harris 1991; J. S. Pearse, pers. comm.). Hand (1955) noted that large clonal aggregations of *A. elegantissima*—some with thousands of individuals, most with fewer—are common in exposed, wave-washed habitats. The two species overlap throughout southern and central California, but *A. sola* is absent from the extensive northern part of the range of *A. elegantissima* (see Francis 1979). Clones of *A. elegantissima* extend along the west coast of North America north to Alaska (Hand 1955) and south at least to central Baja California (McFadden et al. 1997).

So far, no simple, diagnostic difference in morphology allows us to distinguish a polyp of *A. elegantissima* lacking traces of fission (because it had not yet divided or had not done so recently) from a small individual of *A. sola*. The cnidae in each tissue are the same, and the size ranges of each of our categories overlap in the two species. Like the observed differences in color-type frequencies (Francis 1979) and allozyme frequencies (McFadden et al. 1997), differences in the cnidae are apparent only at the population level. Any species-specific differences in the sizes of cnidae are so far obscured by within-species variability. Nonetheless, the fact that cnidae are generally larger in the larger, non-clonal polyps of *A. sola* than in the smaller, clonal polyps of *A. elegantissima* invites closer inspection of the relationship between cnida size and body size both within and between species of many sea anemones.

Genetic evidence that Anthopleura sola *is a species*.—Reproductive isolation between the solitary and aggregated anemones was first inferred from differences in frequencies of color markings in populations in southern and central California (Francis 1979). This analysis demonstrated large and highly significant frequency differences between solitary and aggregated anemones from the same sites against a background of within-species variation that increased with geographic distance. Assuming that the color polymorphism is genetically determined and selectively neutral, this result indicates reduced gene flow (if any) between the species. Using standard electrophoretic methods, no fixed differences were found in allozyme electromorphs of *A. sola* and *A. elegantissima* collected from the same sites in La Jolla and Santa Cruz, California; but there were significant frequency differences between the species at the polymorphic locus complex coding for phosphohexose isomerase (Walsh 1981c, L. Francis, P. J. Walsh, & G. Somero, in litt., L. Francis & D. Hedgecock, in litt.).

Smith & Potts (1987) concluded that their electrophoretic allozyme data yielded no evidence of restricted gene flow between the two forms, which they therefore considered a single species. This negative outcome was attributed by McFadden et al. (1997) to limited sampling (small numbers of individuals and few sites in a restricted geographic range) and to pooling of samples from different locations. In their own allozyme study, McFadden et al. (1997) sampled the full range of sympatry of the two forms, doubling the number of sites and individuals (compared to Smith & Potts 1987), and demonstrated significant differences in allele frequencies between solitary and aggregated forms at every site. Populations of aggregated anemones from sites >1000 km apart were more similar to each other (in terms of genetic distance) than to solitaries from the same sites. McFadden et al. (1997) concluded that the aggregated and solitary anemones represent distinct

sister taxa, referring to them as *A. elegantissima* and *Anthopleura* sp., respectively. The latter we now formally designate as *Anthopleura sola*, new species.

A similar case of sea anemones along the Pacific coast earlier identified as a single species also proved to involve a sibling-species pair. In *Metridium senile*, genetic analysis and life-history studies (Bucklin & Hedgecock 1982, Bucklin 1987) established that the smaller, clonal individuals were distinct from the larger, non-clonal ones, later designated as *M. giganteum* Fautin et al., 1989. Although a study of British populations of large, subtidal vs. small, clonal, intertidal individuals of *M. senile* revealed no genetic evidence of reproductive isolation between the two (Bucklin 1985), the history of research using allozymes in *Anthopleura* spp. suggests that the relatively small differences of recent speciation events can go undetected. Other examples of cryptic actinian species documented by a combination of life-history and genetic differences have involved species of *Sagartia* (see Shaw et al. 1987) and *Epiactis* (see Edmands 1995).

Relationship of A. sola *and other species of* Anthopleura.—*Anthopleura artemisia* was reported by Walsh (1981c) and by Smith & Potts (1987) to be the sister species of *A. sola* + *A. elegantissima*. Some more recent molecular evidence, based on 28S rRNA, 16S rRNA, and COIII sequences, indicates that *A. artemisia* is not closely related to the other eastern Pacific species of *Anthopleura*, but instead belongs to an Asian clade (Walton 1998, J. B. Geller, in litt.). In the same data of Walton and Geller, *A. xanthogrammica*, *A. elegantissima*, and *A. sola* appeared as an unresolved trichotomy in most trees (Walton 1998, J. B. Geller, in litt.). The three species were each separated by fixed changes in one or two base pairs in each gene. However, many features such as coloration, cnidae, the morphology of the mouth, column, and pedal disc, as well as the data of Walsh (1981c) and Smith & Potts (1987), indicate a closer relation-

ship of *A. sola* to *A. elegantissima* than to either *A. xanthogrammica* or *A. artemisia*. For example, small, cylindrical basitrichs (Fig. 2c, d) are present in the pharynx of both *A. sola* and *A. elegantissima* but absent from *A. xanthogrammica*, as well as from *A. artemisia* and other local actiniids (see Hand 1955). Thus, while not excluding the possibility of other topologies, we conclude that *A. sola* and *A. elegantissima* are sibling species.

Acknowledgments

Literature Cited

Annett, C., & R. Pierotti. 1984. Foraging behavior and prey selection of the leather seastar *Dermasterias imbricata*.—Marine Ecology Progress Series 14:197–206.

Barry, J. P., C. H. Baxter, R. D. Sagarin, & S. E. Gilman. 1995. Climate-related, long-term faunal changes in a California rocky intertidal community.—Science 267:672–675.

Brandt, J. F. 1835. Prodromus descriptionis animalium ab H. Mertensio observatorum, Akademiia nauk, Leningrad. Recueil des actes de la séance publique de l'académie impériale des sciences de St. Pétersbourg, 1835, pp. 201–275.

Braun, E., & V. Brown. 1966. Exploring Pacific coast tide pools. Naturegraph Co., Healdsburg, California, 56 pp.

Buchsbaum, V. M. 1968. Behavioral and physiological responses to light by the sea anemone *Anthopleura elegantissima* as related to its algal endosymbionts. Ph.D. dissertation, Stanford University, Stanford, California, 100 pp.

Bucklin, A. 1985. Biochemical genetic variation, growth and regeneration of the sea anemone, *Metridium*, from British shores.—Journal of the Marine Biological Association U.K. 65:141–157.

———. 1987. Growth and asexual reproduction of the sea anemone *Metridium*: comparative laboratory studies of three species.—Journal of Experimental Marine Biology and Ecology 110:41–52.

———, & D. Hedgecock. 1982. Biochemical genetic evidence for a third species of *Metridium* (Coelenterata: Actiniaria).—Marine Biology 66:1–7.

Cutress, C. E. 1949. The Oregon shore anemones (Anthozoa). Masters thesis, Oregon State College, Corvallis, 71 pp.

Dana, J. D. 1846. Zoophytes. United States Exploring Expedition. During the Years 1838, 1839, 1840, 1841, 1842. Under the command of Charles Wilkes, U.S.N., Volume 7. Lea and Blanchard, Philadelphia, 740 pp.

Davis, C. 1991. California reefs. Chronicle Books, San Francisco, 109 pp.

Duchassaing de Fonbressin, P., & G. Michelotti. 1860. Mémoire sur les Coralliaires des Antilles. Imprimerie Royale, Turin, 89 pp.

Edmands, S. 1995. Mating systems in the sea anemone genus *Epiactis*.—Marine Biology 123:723–733.

Fautin, D. G., A. Bucklin, & C. Hand. 1989. Systematics of sea anemones belonging to the genus *Metridium* (Coelenterata: Actiniaria), with a description of *M. giganteum* new species.—Wasmann Journal of Biology 47(1–2):77–85.

Ford, C. E. 1964. Reproduction in the aggregating sea anemone, *Anthopleura elegantissima*.—Pacific Science 18:138–145.

Francis, L. 1973a. Clone specific segregation in the sea anemone *Anthopleura elegantissima*.—Biological Bulletin 144:64–72.

———. 1973b. Intraspecific aggression and its effect on the distribution of *Anthopleura elegantissima* and some related sea anemones.—Biological Bulletin 144:73–92.

———. 1979. Contrast between solitary and clonal lifestyles in the sea anemone *Anthopleura elegantissima*.—American Zoologist 19:669–681.

———. 1988. Cloning and aggression among sea

anemones (Coelenterata: Actiniaria) of the rocky shore.—Biological Bulletin 174:241–253.

Gotshall, D. W. 1994. Guide to marine invertebrates, Alaska to Baja California. Sea Challengers, Monterey, California, 105 pp.

Haderlie, E. C., C. Hand, & W.B. Gladfelter. 1980. Cnidaria (Coelenterata): The sea anemones and allies. Pp. 40–75 in R. H. Morris, D. P. Abbott, & E. C. Haderlie, eds., Intertidal invertebrates of California. Stanford University Press, Stanford, California.

Hand, C. 1954. The sea anemones of central California. Part I. The corallimorpharian and athenarian anemones.—Wasmann Journal of Biology 12(3):345–375.

———. 1955. The sea anemones of central California. Part II. The endomyarian and mesomyarian anemones.—Wasmann Journal of Biology 13(1):37–99.

———. 1975. Class Anthozoa. Pp. 85–94 in R. I. Smith & J. T. Carlton, eds., Light's manual: intertidal invertebrates of the central California coast, 3rd edition. University of California Press, Berkeley, California.

Harris, L. G. 1991. Comparative ecology of subtidal actiniarians from the coasts of California and the Gulf of Maine, USA.—Hydrobiologia 216/217:271–278.

Hedgpeth, J. 1962. Introduction to seashore life of the San Francisco Bay region and the coast of northern California. University of California Press, Berkeley, 136 pp.

———, & S. Hinton. 1961. Common seashore life of southern California. Naturegraph Co., Healdsburg, California, 64 pp.

Hinton, S. 1969 and 1987. Seashore life of southern California. An introduction to the animal life of California beaches south of Santa Barbara, 1st and 2nd editions. University of California Press, Berkeley, 181 pp. and 217 pp.

Jennison, B. L. 1979. Gametogenesis and reproductive cycles in the sea anemone Anthopleura elegantissima (Brandt, 1835).—Canadian Journal of Zoology 57:403–411.

Johnson, M. E., & H. J. Snook. 1935. Seashore animals of the Pacific coast. Macmillan Co., New York, 659 pp.

MacGinitie, G. E., & N. MacGinitie. 1949 and 1968. Natural history of marine animals, 1st and 2nd editions. McGraw Hill Book Co., New York, 474 pp. and 523 pp.

McFadden, C. S., R. K. Grosberg, B. B. Cameron, D. P. Karlton, & D. Secord. 1997. Genetic relationships within and between clonal and solitary forms of the sea anemone Anthopleura elegantissima revisited: evidence for the existence of two species.—Marine Biology 128:127–139.

Pearse, J. S. 1981. Intertidal animals. Chapter 5, pp. 205–236 in B. J. Le Boeuf and S. Kaza, eds.,

The natural history of Año Nuevo. Boxwood Press, Pacific Grove, California.

———, V. B. Pearse, & A. T. Newberry. 1989. Telling sex from growth: dissolving Maynard Smith's paradox.—Bulletin of Marine Science 45:433–446.

Rafinesque, C. S. 1815. Analyse de la Nature, ou Tableau de l'Univers et des Corps Organisés. Published by the author, Palermo, 224 pp.

Ricketts, E. F., & J. Calvin. 1968. Between Pacific tides, 4th edition. Revised by J. W. Hedgpeth. Stanford University Press, Stanford, California, 614 pp.

———, ———, & J. W. Hedgpeth. 1985. Between Pacific tides, 5th edition. Revised by D. W. Phillips. Stanford University Press, Stanford, California, 652 pp.

Sagarin, R. D., J. P. Barry, S. E. Gilman, & C. H. Baxter. 1999. Climate-related change in an intertidal community over short and long time scales.—Ecological Monographs 69(4):465–490.

Sebens, K. P. 1981. Reproductive ecology of the intertidal sea anemones Anthopleura xanthogrammica (Brandt) and A. elegantissima (Brandt): body size, habitat, and sexual reproduction.—Journal of Experimental Marine Biology and Ecology 54:225–250.

Secord, D. L. 1995. Host specificity and symbiotic interactions in sea anemones. Ph.D. dissertation, University of Washington, Seattle, Washington, 89 pp.

———, & L. Augustine. 2000. Biogeography and microhabitat variation in temperate algal-invertebrate symbioses: zooxanthellae and zoochlorellae in two Pacific intertidal sea anemones, Anthopleura elegantissima and A. xanthogrammica.—Invertebrate Biology 119:139–146.

Shaw, P. W., J. A. Beardmore, & J. S. Ryland. 1987. Sagartia troglodytes (Anthozoa: Actiniaria) consists of two species.—Marine Ecology Progress Series 41:21–28.

Shick, J. M., W. C. Dunlap, & A. K. Carroll. 1996. Mycosporine-like amino acids and small-molecule antioxidants in Anthopleura spp.: taxonomic and environmental patterns.—American Zoologist 36(5):72A.

Smith, B. L., & D. C. Potts. 1987. Clonal and solitary anemones (Anthopleura) of western North America: population genetics and systematics.—Marine Biology 94:537–546.

Snyderman, M. 1987. California marine life. Marcor Publ., Port Hueneme, California, 255 pp.

———. 1998. California marine life. Roberts Rinehart Publ., Niwot, Colorado, 180 pp.

Stephenson, T. A., & A. Stephenson. 1972. Life between tidemarks on rocky shores. W. H. Freeman, San Francisco, 425 pp.

Tsuchida, C. B., & D. C. Potts. 1994. The effects of illumination, food, and symbionts on growth of the sea anemone *Anthopleura elegantissima* (Brandt, 1835) 2. Clonal growth.—Journal of Experimental Marine Biology and Ecology 183: 243–258.

Walsh, P. J. 1981a. Purification and characterization of glutamate dehydrogenases from three species of sea anemones: adaptation to temperature within and among species from different thermal environments.—Marine Biology Letters 2:289– 299.

———. 1981b. Purification and characterization of two allozymic forms of octopine dehydrogenase from California populations of *Metridium senile*.—Journal of Comparative Physiology 143: 213–222.

———. 1981c. Temperature adaptation in sea anemones (Anthozoa; Cnidaria): molecular mechanisms and evolutionary perspectives. Ph.D. dissertation, University of California, San Diego, La Jolla, California, 150 pp.

Walton, E. D. 1998. Phylogenetic analysis of reproductive modes in the genus *Anthopleura*. Masters thesis, University of North Carolina at Wilmington, North Carolina, 58 pp.

Wasson, K., & A. T. Newberry. 1997. Modular metazoans: gonochoric, hermaphroditic, or both at once?—Invertebrate Reproduction and Development 31:159–175.

Williams, R. B. 1996. Measurements of cnidae from sea anemones (Cnidaria: Actiniaria): statistical parameters and taxonomic relevance.—Scientia Marina 60(2–3):339–351.